

A MODEL TO PREDICT DENSITY AND
DIVERSITY OF BREEDING BIRDS IN THE
PONDEROSA PINE FOREST

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A Model to Predict Density and
Diversity of Breeding Birds in the
Ponderosa Pine Forest

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Introduction

The organization of biological communities has long been of interest to ecologists and within the last decade avian ecologists have provided a great deal of descriptive information and ecological theory about avian communities. Studies on avian communities can be divided into two types; those that describe what the avian community consists of, and those that attempt to find the underlying causes for why such an organization exists. Data from the first type provide for the needs of the second. Both are necessary and important in the determination of broad, general patterns.

On a broad geographic scale historical considerations such as centers of origin, barriers to dispersal, and broad climatic patterns can all be used as explanations. Many species of birds do not breed in a specific habitat simply because they have never encountered it.

On specific sites, such as the ponderosa pine forest, the question becomes, What prompts a particular bird to select a specific location or area for a territory and breeding site? Early work by Beecher, 1942, Kendeigh, 1945, Lack 1933, and others concluded that the more complex the habitat, the more complex the avian community. The pioneering efforts by McArthur and his co-workers in the early and mid-sixties gave this search for underlying causes its first theoretical framework. There is now little doubt the concepts such as foliage diversity and patchiness help define the complexity of different community types. Within a specific community-type, however, the use of foliage height diversity and patchiness does not predict community organization (Willson 1974, Tomoff 1974, Carothers et al., 1974, Szaro and Balda 1979) and a finer subdivision of habitat variables may be necessary to explain patterns in avian communities. To predict community structure (density, diversity, presence) within a specific habitat one may have to use a multiple

of variables that may be used singly or in combination by the breeding birds. Obviously, this will not be a simple single-factor analysis and the selection of factors will at first be broad and somewhat random, for in many cases we will have to use "best guesses" to select the factors. As Karr (1980) points out, temperature-moisture regimes, seasonality, vegetation structure, food resources, interspecific coevolutionary forces, and resource utilization patterns, all may interact in a complex manner to determine community structure.

Because of the complexity of the problem and the large numbers of data sets of bird populations plus attendant variables needed for such an analysis few models have been developed that have predictive strength over broad regions and/or over long time spans. Thus, forest managers have little information available to them to accurately assess the impact of various management on non-game birds. With the increase demand for fuel and timber from our national forests it will become increasingly important to understand the effects of these activities on non-game birds.

This report will attempt to provide a qualitative model with predictive value for the ponderosa pine forest. Forest managers can then assess the relative modifications of the bird community as related to the degree of modification of the plant community.

Methods and Materials

Bird-vegetation-climatic data used to develop this model have been collected for 21 different breeding-bird years on study sites in north-central Arizona (Table 1). A breeding-bird year is defined as the breeding bird densities from a single study plot for a single year. These data were gathered from seven different pine forest sites that show varying degrees of

tree and understory density. The data base is thus broad (seven different plots) and has depth (minimum of two consecutive years of data from a specific site).

The model concentrates on four general aspects of potential limiting factors that singly and/or in concert can play a key role in determining avian density and diversity. These are described below with the rationale for each:

I) Climatic Factors: These factors can operate in both a direct and indirect manner. Fretwell (1972) emphasizes the direct affect of winter climate on the overwinter survival of permanent resident species. If the winter climate is mild survival may be high and spring breeding populations should be high. Harsh winters may result in depressed spring populations. Also, during years of high breeding densities populations may demonstrate a more broad habitat selection, using both optimal and suboptimal habitats, than in low density years. Then only optimal habitats will be occupied. The affects of weather are known to be different on ponderosa pine forest plots which have been treated differently (Szaro and Balda, MS). Delayed breeding due to a harsh spring combined with early summer rains could place nestlings and fledglings under an extreme selective pressure. Fretwell (1972) cautions that physical (and biotic) factors on the wintering ground of summer residents can also affect breeding bird densities the next spring. This direct factor is obviously impossible to incorporate into our model.

Indirect affects of climate are more elusive but never-the-less important. Most breeding species in the ponderosa pine forest are insectivorous during the breeding season. Insect production is probably closely related to the temperature-moisture regime. Dry, cool to cold springs are probably not as productive as moist, warm springs. Understory density and diversity is also affected which may in turn affect thermal refugia, berry and nectar production,

and predator escape cover. Production of pine seeds, acorns, and juniper berries is also climate dependent. These differences in production may be reflected in the bird populations.

Ten factors of weather were examined as possible predictors of the overall breeding densities, guild density, and species diversity with step-wise multiple regression analysis. These factors were: 1) SNOW-precipitation as snow; 2) RAIN-precipitation as rain; 3) RAIN PLUS SNOW; 4) WIN. PRECIP.-winter precipitation; 5) TOT.-total precipitation; 6) JANMX-maximum January temperature; 7) JANMN-minimum January temperature; 8) WNAVE-winter mean daily temperature; 9) MEAN-yearly mean daily temperature; and 10) RANGE-temperature range during the previous July to January. These data were supplied to us by the Rocky Mountain Forest and Range Experimental Station, Beaver Creek Project.

II) Vegetation Configuration: Historically vegetation structure has been strongly linked to avian community organization as mentioned earlier. The concept of the "niche gestalt" based on characteristics of vegetation has been clearly demonstrated with multivariate techniques by James (1970) Anderson and Shugart (1974) and others. Recently Holmes et al. (1979) suggested a finer focus on avian resources such as plant species composition, height characteristics, branching patterns, and specific foraging sites rather than the more general approach that has been used in the past.

Eleven factors of foliage structure were examined as possible predictors of bird density and diversity. These factors were: 1) FVONE-foliage volume 0-2 meters; 2) FVTWO-foliage volume 0-4 meters; 3) FVTOT-total foliage volume for all strata; 4) SAP-sapling volume; 5) TRNK-trunk volume; 6) OAK-oak foliage volume; 7) IVPON-ponderosa pine importance value; 8) IVOAK-oak importance value; 9) SNAG-s snag density; 10) TREES-absolute density of all trees; and 11) RATIO-proportion of oak foliage volume to total foliage volume. These data were gathered according to the techniques described by Szaro and Balda (1979).

III) Special Habitat Requirements of Secondary Cavity Nesting Species:

Secondary cavity nesting species have very specific habitat requirements in that they nest only in holes or crevices which normally occur only in dead trees. Earlier we demonstrated that the densities of 10 secondary cavity nesters in the ponderosa pine forest showed a positive, significant relationship with snag density ($r^2 = 76\%$) (Cunningham, Balda, and Gaud 1980). We could not, however, account for the changing densities of individual species in the above work.

In order to differentiate the effects of habitat alteration on the breeding densities of the secondary cavity nesting species we use 18 breeding-bird years and 11 vegetative variables from six studies sites that had the appropriate data available. These data were used in multiple regression analysis. The variables found to be important predictors were: 1) FV-foliage volume of ponderosa pine; 2) SD-snag density; 3) SSV-foliage volume of shrubs and saplings; 4) MA-mean area occupied by an individual type; 5) MD-mean distance between trees; and 6) ADP-absolute density of ponderosa pines. These data were gathered as described by Szaro and Balda (1979).

IV) Relative Effects of Interspecific Competition: Szaro and Balda (1979) divided the breeding birds of the ponderosa pine forest into four foraging guilds (Table 2). A guild is defined as a group of species that have common foraging techniques and therefore contains prime candidates for interspecific competition (Root 1967). Species in the same foraging guild might show reciprocal changes in density between years if competition for some limited resource was occurring, and if any pair of species fill all usable habitat. If such is the case then for each increase in breeding pairs for one of the species there should be a corresponding decrease in density of the other species.

The major assumption of a full habitat, however, has certain problems

associated with it. Between year differences might be such that the habitat expands or restrictions are relaxed so that both species of a pair can increase or decrease with changing conditions.

In order to test for reciprocal density changes, partial correlation coefficients were obtained for each species within a guild when compared to all possible combinations of species within the guild until the variance contributed by all but one species was accounted for. If members of a foraging guild are competing and the above assumptions are not violated one should see a preponderance of negative correlation coefficients. Data used for this analysis were taken from Szaro and Balda (1979).

Results

I. Climatic Factors: Multiple regression models were first devised for climatic variables alone. This was done primarily to gain an insight as to how climatic variables alone affect bird populations, as these factors are obviously beyond the control of forest managers. For this analysis we used only three study plots (Watersheds 13, 14, 17) for which we have complete weather and bird data from three consecutive years. These three plots show varying degrees of modification from severely thinned (WS17) to uncut (WS13) (see Szaro and Balda, 1979).

Climatic variables alone accounted for over 99% of the variability in total breeding bird densities on all three watersheds. Total breeding bird density was highly correlated with snowfall amounts in one case (WS14) and winter mean daily temperature in two cases (Tables 3, 4, 5).

For each foraging guild the designated model explained over 98% of the variability in density. The picker-gleaner guild was especially sensitive to winter temperature patterns. The ground feeding guild responded to winter

temperatures and rainfall. The pecker-hammerer-tearer guild responded negatively to precipitation variables and positively to winter mean daily temperature. Hawkers-hoverers, and aerial feeders respond in a somewhat similar manner. No guild responded significantly to the same climatic factor on the different study areas.

Differences existed among the study plots in regards to the types of climatic factors that proved important in explaining the variability in breeding bird density. On watershed 17 all five significant climatic variables were ones that occurred during the winter season. On watershed 14 four of five significant variables were winter ones, whereas on watershed 13 only three of five were winter ones.

Of the ten possible climatic variables used in the multiple regression analysis, seven turned out to have predictive value. Three of the seven were temperature variables and the other four were precipitation variables. A particular variable could have appeared up to 15 times (three watersheds times five bird density classes). Winter mean daily temperature appeared in the models six times, snowfall three times and maximum January temperature twice. The other four variables appeared only once each.

Interesting differences existed as to how (positively or negatively) the variables affected total and guild densities. Temperature variables, as a group occurred in nine of 12 possible models and did so positively eight times. This difference is significant ($P = .04$) with the binomial test when $p = q = 1/2$. Moisture variables occurred in six out of 15 possible models and were always negatively associated with total and guild density. This difference is also significant ($P = .02$) with the binomial test when $p = q = 1/2$.

II. Vegetation Structure and Climatic Patterns: Multiple regression models were developed from the 21 breeding years and 21 independent vegetation-climate

variables. Models were developed for the four foraging guilds, four nesting guilds (cavity and depression nesters, foliage nesters, ground nesters,) total bird density, and total bird diversity (number of breeding species).

Five independent variables contributed significantly to the model to predict total breeding bird density. Four of the variables were structural in nature and one was climatic (Table 6). The two most important variables were total folige volume and trunk volume. The former was positively related to bird density and the latter negatively so. The model explained over 86% of the variability in total bird density.

Two climatic variables were significantly predictors of breeding bird diversity (here defined as the total number of breeding species per plot). Precipitation as snow and temperature range from previous July through January, both can be considered winter variables. Both had a negative affect on species diversity (Table 6).

Because both of these variables are influencial during the winter months it is unclear if our results show the affects of winter weather on only permanent residents which directly experience them or also on summer residents. In the latter case the affect could be either direct, or indirect. Late winter snows could deter the birds from using the area to breed, and insect populations may be low because of cold temperatures and heavy snows during the preceeding winter.

Using those study sites for which we have three consecutive years of data (Watersheds 13, 14, 17) we scored each species as present or absent for the three years. Species were divided into permanent resident and summer residents. Changes in presence were then tabulated. Each species could change its presence a maximum of two times (between 1973 and 1974 and also between 1974 and 1975). Percent of possible changes and percent of possible species that changed were then calculated.

Four permanent resident species (Acorn Woodpecker, Mountain Chickadee, Pygmy Nuthatch and Steller's Jay) showed changes in presence and 11 summer residents (Mourning Dove, Common Nighthawk, Broad-tailed Hummingbird, Say's Phoebe, Violet-green Swallow, House Wren, Hermit Thrush, Yellow-rumped Warbler, Western Tanager, Hepatic Tanager and Black-headed Grosbeck) did likewise. No patterns emerged from these lists of species.

Changes related to amount of disturbance were, however, evident. The number of permanent resident species disappearing and then reappearing decreased as the habitat became less disturbed. Watershed 17, for example, had twice the changes and species changes than did uncut Watershed 13. Just the opposite occurred with the summer residents. Watershed 13 and 14 had nine species (summer resident species) (30 percent) change presence whereas only five (21 percent) did so on Watershed 17 (Table 7).

More specific models were tested to predict densities of the four foliage guilds and three nesting guilds. Obviously the same species and their densities are incorporated into both sets of models but the species are shuffled differently into the groups. Selected significant predictors for the foraging guilds explained between 60 and 88 percent of the variability in nesting density (Table 8). Models for the nesting guilds explained between 62 and 87 percent of the variability in nesting density (Table 9).

Five significant predictors accounted for 88 percent of the variability in nesting density for the picker-gleaner guild. The three most important variables were total foliage volume trunk volume and snag density (Table 8).

Using the 21 vegetation-climate variables only 60 percent of the variability in the density of ground feeding birds could be explained. The two significant variables were ponderosa pine importance value and precipitation as snow (Table 8). This is the weakest model developed in the study.

Our multiple regression model for the peckers, hammerers and tearers

explained 63 percent of the variability in nesting density. All three significant variables in the model were climatic ones (Table 8).

Five significant variables accounted for 84 percent of the variability in nesting density of the hawkers, hoverers, and aerial feeders. Ponderosa pine importance value was the most important variable and the only vegetation variable to immerge in the model. The other four variables; precipitation as snow, yearly mean temperature, winter mean daily temperature, and minimum January temperature explained lesser amounts of the variability in nesting density (Table 8).

When the bird species were arranged by nesting guild the range of variability explained by the significant predictors was between 62 and 93 percent.

The best model for a nesting guild was found for the cavity and depression nesters. For this guild five significant predictors explained 93 percent of the variability in nesting density. The most important predictor was oak importance value followed by trunk volume, sapling volume, winter mean daily temperature and snag density (Table 9). More will be said about this group later as a specific set of variables was used to look at specific species.

For the foliage nesting guild, 69 percent of the variability in nesting density was explained by our model. One climatic variable (precipitation as snow) and three vegetation variables (ponderosa pine importance value, proportion of oak to total foliage volume and total foliage volume) contributed significantly to the model (Table 9).

Four significant variables explained 62 percent of the variability in nesting density of the ground nesting guild. Two predictors were climatic and two were vegetation variables. The most important of these was ponderosa pine importance value (Table 9).

III. Special Habitat Features Required by Secondary Cavity Nesting Species:

Because of the special and unique needs of secondary cavity nesters and also

our presumed knowledge of these birds we attempted to select specific variables for species specific models. These models used only structural variables in order to get a preliminary estimate of the value of attempting such an approach with these six sensitive species. Densities of five of the six species were then modeled using all 21 variables.

The most important predictors for the densities of the Violet-green Swallow, Pygmy Nuthatch and Mountain Chickadee were foliage volume and snag density (Table 10). Snag density and shrub and sapling volume were important predictors of Brown Creeper densities. Western Bluebird apparently respond to the absolute density of pines, mean area occupied by a tree and mean distance between trees, but not snags. The White-breasted Nuthatch did not respond to any of the variables in a significant manner. Snags played little, if any, role in explaining the variability in densities of the White-breasted Nuthatch and Western Bluebird (Table 10).

Excluding the White-breasted Nuthatch the six vegetation variables explained a highly significant amount of the fluctuation in breeding densities of the five species. This ranged from 78 percent for the Western Bluebird to 94 percent for the Violet-green Swallow (Table 10).

Ninety-three percent of the variability in nesting density was explained by five independent variables for the cavity and depression nesters as a group. Snag density was a modest but significant variable (Table 9). For individual species, however, the independent variables varied.

The Mountain Chickadee model included five significant predictors. Snag density and oak foliage volume were the most important (Table 10).

For the Pygmy Nuthatch, one of the most dense breeding species in the ponderosa pine forest, 83 percent of breeding density was explained by three significant vegetation variables. Total foliage volume and snag density contributed most to the model (Table 11).

Four vegetation variables combined to explain 94 percent of the variability in nesting density of the Violet-green Swallow. The two most important variables were oak importance value and trunk volume. All four predictors were negatively associated with breeding density (Table 10).

No vegetative variable contributed significantly to the model that explained 55 percent of the fluctuations in breeding density of the Western Bluebird. The most important variable was maximum January temperature (Table 11).

The poorest model was for the White-breasted Nuthatch. Two significant independent variables explained only 36 percent of the fluctuation in breeding density. These were total foliage volume and yearly mean daily temperature. Thus, like the earlier described vegetation model, densities of the White-breasted Nuthatch defies modeling at a high degree of predictability using the present independent variables (Table 11).

IV. Other Species Specific Models: In addition to the species specific models described above the densities of another five species were also modeled. These were selected as representatives of the ponderosa pine forest and also of the designated guilds. All achieved measurable densities on most plots in most years of the study. Step-wise multiple regression models explained a high amount of variability in the nesting density of the Gray-headed Junco, a ground foraging, ground nesting bird and Steller's Jay, a member of the pecker, hammerer, and tearer foraging guild and the foliage nesting guild. Significant, but unexciting models were constructed for the Solitary Vireo, Hairy Woodpecker, and Chipping Sparrow (Table 12).

The Gray-headed Junco responded negatively to oak importance value, trunk volume, sapling volume and precipitation in the form of snow. No independent variables were positively associated with the density of this ground foraging and nesting species.

The Steller's Jay, the largest permanent resident in the ponderosa pine forest, had densities that were positively associated with absolute density of trees and negatively associated with snag density and oak foliage volume.

V. Effect of Interspecific Competition: If birds within guilds are competing for a limited resource and the total population occupies all available habitat then when the population of one species increases, the populations of other species must decrease.

A total of seven species were assigned to the picker and gleaner guild, thus 21 partial correlation coefficients were obtained (Table 13). Sixteen of these had a positive sign and five had a negative correlation. Statistical significance at the five percent level was achieved in only three of the 21 couplets. Two of these couplets (White-breasted Nuthatch and Solitary Vireo; Yellow-rumped {Audobons'} Warbler and Western Tanager) were positive in sign indicating these pairs of species actually track the variability in weather and folige in a similar fashion. One couplet (Pygmy Nuthatch and Solitary Vireo) showed a significant negative correlation. As one species increased in density the other responded with a decrease in density.

Five species were included in the peckers, hammerers, and tearers guild. Of the ten couplets, seven had positive correlation coefficients and three had negative ones. The Common Flicker-Hairy Woodpecker couplet had a statistical significant positive correlation (Table 14). The Steller's Jay-Black-headed Grosbeak partial correlation coefficient was almost significant (.071) and was also positive.

In the aerial, hawking, and hovering guild 15 partial correlation coefficients were generated for the six species. Eight of these were positive and seven were negative. Three positive partial correlation coefficients achieved statistical significance (Common Nighthawk and Broad-tailed Hummingbird; Western Bluebird and Western Wood Pewee; Western Flycatcher and Violet-green

Swallow) (Table 15). No negative correlations were significant.

The six species in the ground feeding guild had eight positive correlation coefficients and seven negative ones. One positive correlation coefficient was significant (Robin and Chipping Sparrow) (Table 16). No negative correlation coefficients approached an acceptable significance level.

Discussion

The results of our step-wise regression models for the guilds, total density, and bird diversity indicate that both biotic (forest structure) and abiotic (climatic factors) play a complex role in determining avian community structure. These two factors, however, may influence community structure in very different ways. We can make predictions, that in a plant community such as the ponderosa pine forest the structure of the forest should be most important as a selector of what species can possibly nest there. That is, the number of potentially different ecological niches present will be a primary function of forest structure. Because of the nature of this coniferous forest, most of the potential niches should be present every year because the forest structure does not change drastically between years. A secondary function is possibly the number of similar niches present. The primary function of climatic factors may be through its influence on productivity. The warmer the temperatures and the higher the precipitation the greater the productivity to support the avian community. This will result in a higher density of birds. As climatic factors vary from year-to-year different species with special adaptations for feeding on certain prey items may be "favored". Some ground feeding finches on the Galapagos Islands may show this response with one species being abundant during dry periods and another during wetter years (Grant and Boag 1980). Weins (1974) has shown the same pattern for western

grassland birds.

Because it is impossible to equate a change in temperature or variation in precipitation with a change in foliage structure Szaro and Balda (MS) used cluster analysis to separate the effects of biotic and abiotic factors on the breeding bird community of the ponderosa pine forest. Breeding bird densities clustered by forest-type rather than year. Three broad clusters resulted: the clear cut area, heavily treated areas, lightly treated and the control area. These three clusters reflect the effect of habitat alteration rather than the year-to-year effect of weather conditions.

The above statements would support hypotheses that climatic variables are most important in controlling avian densities and biotic ones for species diversity. Tables 3, 4, and 5 show that using only weather variables, winter mean daily temperature and total snowfall can explain 99 percent of the variability in total bird density. This trend does not hold, however, when biotic factors are taken into consideration (Table 6). Now, biotic variables become much more important in explaining total bird density than do abiotic ones. In contrast, abiotic factors are much more important in explaining species diversity as precipitation as snow and temperature range during the previous July through January explaining 69 percent of the variability is species diversity. Both can be viewed as winter variables and both had a negative affect on species diversity.

For permanent resident species, diversity varied more on the severely thinned plot than it did on the uncut control area (Table 7). Thus, winter climate may have the direct affect of reducing permanent resident species on ponderosa pine forests that are heavily cut. These areas may be of a foliage configuration that is not conducive to modifying and buffering the harsh winter climate. The sparce tree cover may not be able to curtail wind speed, and large day-night temperature differentials, among other things.

Summer resident species acted in just the opposite manner as they showed higher variability of diversity on the more lightly cut and uncut areas. Because of the denser canopy, temperatures are cooler and snow remains longer in these areas. Phenological events (germination of annuals, budding and leafing out of shrubs, etc.) occur later on the more natural areas than on the severely thinned areas. The affect may be that it deters summer resident species from settling in these areas to breed, and they look elsewhere for more suitable breeding territories. This suggests that site tenacity (philopatry) is not well developed in summer residents of the ponderosa pine forest. These birds may be opportunistic in their use of the ponderosa pine forest and settle wherever favorable breeding conditions exist. No studies have addressed themselves to this problem to date.

Total bird density was best predicted by four biotic variables and only one abiotic variable. Precipitation in the form of snow again had a significant negative affect. The two most important variables were biotic ones, total foliage volume and trunk volume. But, the sign of the former was positive whereas that of the latter was negative. Usually when a forest has high trunk volume it also contains high foliage volume. These characteristics are common in areas that have been undisturbed for many years such as the Pearson Natural Area and Watershed 13 of this study. High trunk volume may be indicative of a senescent or over-aged forest. Szaro and Balda (MS) have shown that pair-packing is less pronounced in old uncut stands. But regression analysis revealed that foliage volume was positively associated with total bird density. Thus, the answer must lie in the distribution of the foliage. Large trunk volume indicates very tall trees with large amounts of foliage high above the ground. Only two species of birds (Pygmy Nuthatch and Grace's Warbler) consistently use these vertical sections of the foliage (Balda 1969). Of the three species that breed only in dense ponderosa pine forests (Red-faced Warbler,

Hermit Thrush, Western Flycatcher), only the Red-faced Warbler feeds high in the trees. All three of these species also reach much higher densities in the mixed coniferous forest. Thus, old, uncut, unburned forests do not support higher overall bird densities than do lightly cut areas.

Snag density appeared as a significant positive predictor of overall breeding bird density. The reasons for this may be that cavity and depression nesters make up a rather large segment of the total breeding birds (25-30 percent) (Balda 1975). Snags also provide foraging substrate for other species as well (Szaro and Balda 1979).

Oak importance value (the sum of relative density, relative frequency, relative dominance) was also a significant predictor but did so in a negative fashion. The use of oak with its different life form may be difficult for birds adapted to the very specific habitat limitations of this monoculture. Thus oak may not be viewed as prime foraging habitat by the breeding birds. Such is also the case with juniper in the pine-oak woodland of southern Arizona (Balda 1969). Because of its unique life form, however, oak could provide requisites for a few of the species present such as the White-breasted Nuthatch and Red-faced Warbler.

Models to predict the densities of specific foraging guilds differ in the amount of variability they accounted for (Table 8). Five significant variables explained 83 percent of the variability in the pecker and gleaner guild whereas only two significant variables accounted for 60 percent of the variability in density of the ground feeders.

Four biotic and one abiotic variable made significant contributions to the pecker and gleaner model. Total foliage volume was again a positive variable whereas trunk volume was a negative one. The above discussion can also be applied to this case. Precipitation in the form of rain was a significant negative predictor of pecker and gleaner densities. No doubt this was primarily

spring rains which sometimes occur after the winter snows and before the summer drought. Its affect probably was most severe on the summer resident members of this guild. Seven of nine guild members were summer residents. The other two members, Pygmy Nuthatch and Mountain Chickadee were possibly not adversely affected.

Eighty-four percent of the variability in density was explained by five significant variables for the aerial feeding guild (Table 8). Four of these were abiotic and one a biotic factor. The most important variable was ponderosa pine importance value which incorporates relative density dominance and frequency. These birds appear to need an almost pure pine forest in order to reach highest densities. All rely heavily on insects and all are summer residents (Table 2). It is thus of interest that the model contains four climatic variables, three of which are winter occurrences (precipitation in the form of snow, winter mean daily temperature, minimum January temperatures). Precipitation in the form of snow (the second most important variable in the model) was negative as were yearly mean temperature and minimum January temperature. Thus, low winter temperature plus high snow levels somehow repel these insectivorous birds from the forest. This finding is supported by the fact that winter mean daily temperature had a positive influence on aerial feeder density the next spring. Most all of these psecies use the foliage configuration for nesting and for perches to rest, preen, watch for predators, and sight insects. Once the general attributes of a nest and perch site are met by the ponderosa pine then insect density must be most critical. These data then provide convincing evidence that winter weather conditions have a significant affect on spring and early summer insect densities in the ponderosa pine forest.

Only about 60 percent of the variability in density of both the peckers, hammerers, and tearers and ground feeding guild was explained by our models.

For ground feeders, ponderosa pine importance value was the most important variable and the only biotic one to appear. Precipitation in the form of snow as again negatively associated with the density of ground feeders. Most ground feeders in this study were granivorous birds that rely on last years seeds or those produced by early blooming annuals and perennials. Here snow may have the direct physical affect of covering the needed seeds so they may not be available to this group of birds.

All but one of the pecker, hammerer, and tearer guild are permanent residents of the ponderosa pine forest and only three significant variables, all climatic ones contributed significantly to the model. January temperatures appear to be critical to this group, as minimum temperatures during this month had a negative affect on densities and maximum temperatures a positive affect.

When species were arranged by nesting guilds no increase in predictability occurred. Here species were simply placed in categories different from the above ones. Two biotic variables that did not occur in the foraging guild models appeared in the nesting guild models. Both were associated with the presence of oaks. Oak importance value was negatively associated with the densities of the cavity and depression nesters and proportion of oak foliage to total foliage volume was positively associated with the densities of foliage nesters. No new abiotic factors appeared.

As occurred with the climatic models, some interesting patterns emerged in how variables affect bird densities. For both sets of models a total of seven structural variables and eight climatic ones were found significant in one or more models. The four most often occurring vegetation variables were ponderosa pine importance value, snag density, total foliage volume, and trunk volume in that order. For climatic variables the most often occurring predictor was precipitation as snow. This variable appeared more than twice as often as any other climatic variable and was always negative.

How did these two sets of variables affect the bird populations? For the structural variables the signs were predominantly positive, occurring 13 times in this manner and six times as negatives. Two important exceptions did occur. First, trunk volume always was negatively associated with bird densities. As mentioned earlier this seems to reflect an over-age stand. Second, oak importance value was also negatively associated with bird densities. But, because the importance value figure is a combination of three figures (density, dominance, and frequency) it is difficult to explain just what about the oaks affects bird densities in a negative fashion. Of all the vegetation variables used in the nine models only one changed its sign. Sapling volume was positively associated with the density of pickers and gleaners and negatively associated with the density of the cavity and depression nesters.

Temperature and/or moisture variables occurred in all nine models. Whereas foliage variables were predominantly positive in the models, the climatic variables appeared as negatives 12 times and only twice as being positively associated with bird densities. This difference is significant ($P = .012$) with the binomial test when $p = q = 1/2$. As with the weather models described earlier all precipitation factors always were negatively associated with breeding bird densities. Winter mean temperature and maximum January temperatures were each positively associated with breeding bird densities. None of the variables changes signs among the nine models.

Both Weins (1974) and Grand and Boag (1980) show that fluctuations in density of grass and shrubland birds demonstrate positive responses to precipitation. The connecting links are described as one of high amounts of precipitation leading to more plant growth and/or more insects. This is certainly not the case in the ponderosa pine forest. Here the dominant plant species, ponderosa pine responds only slightly to year-to-year variations in precipitation. Insects, however, seem to show a definite negative relationship with winter

precipitation. Thus, higher amounts of precipitation cannot and should not be equated with higher productivity for the birds of this habitat type.

Special Habitat Needs of Secondary Cavity Nesters: Because forest managers cannot manage the weather we used two techniques to model the secondary cavity nesters. One set of models was developed using only biotic features that we deemed important for this group of birds and another using all 21 variables as used in the above models.

For the vegetation model foliage density, snag density, and shrub and sapling volume were the three most important variables. All explained significant amounts of the variability for the Violet-green Swallow, Pygmy Nuthatch, Mountain Chickadee, and Brown Creeper. Neither the Western Bluebird nor the White-breasted Nuthatch responded to these three factors. Using only vegetation variables our models explain a large and significant amount of the variability in nesting density for five of the six species (Table 10). As pointed out by Cunningham et al. (1980) management plans that address themselves only to snag management will ultimately fail. These birds require more than just nest-sites. They require perch sites, and foliage to forage and hide in.

No vegetation variables proved significant to explain the density of the White-breasted Nuthatch. This ubiquitous secondary cavity nester is a very wide ranging species in the ponderosa pine forest. It appears to be mated for life and has exceptionally large territories (pers. obs. R. P. Balda). It is possible that this species is either limited by some biotic or abiotic variable we did not measure by intraspecific social interactions.

The fact that the Violet-green Swallow responds to the square of foliage volume and snag density is not surprising from a biological point-of-view. Most swallows are colonial nesters and thus their overall distribution is highly clumped. The Violet-green Swallow may actually become a colonial nester under

conditions of extremely high snag densities as occurs on some protected areas. There is little doubt that the Violet-green Swallow tends to have a clumped distribution in the ponderosa pine forest (pers. obs. R. P. Balda).

A combination of the biotic and abiotic variables for the five secondary cavity nesters individually showed that each species responded differently to most variables (Table 11), but the total amount of variability explained with this model was surprisingly similar to that explained with only the vegetation variables (Table 10).

The Mountain Chickadee and Pygmy Nuthatch were most consistent in response to variables across models. They responded to snag density and foliage volume in both models. White-breasted Nuthatch densities were predicted by two significant variables in the inclusive model but the overall predictability of these two factors was a low 36 percent (Table 11). The resolution of limiting factors for this species is no clearer with the climatic variables included than it is without them.

Western Bluebird density fluctuations were significantly correlated with three biotic variables in the vegetation test but surprisingly with four abiotic variables in the combined regression. Thus caution must be used in attempting to tailor pine forest for this species.

Seven different independent variables associated with vegetation and a like number of climatic variables affected the species discussed above. The most often reoccurring vegetation predictors were trunk volume, which was always negatively associated with breeding densities, and snag volume, which was always positively associated with breeding densities. This is consistent (as expected) with the models discussed earlier. Three exceptions did occur, however, as total foliage volume which had occurred earlier consistently as a positive variable appeared as a negative one for the White-breasted Nuthatch. Oak foliage volume and foliage volume from 0 to 4M above the ground occurred

for the first time in the Mountain Chickadee model.

The seven climatic variables, the most common of which was precipitation as snow, appeared in a consistent fashion as described above for the more general models. One new variable appeared, that of total precipitation which helped explain the variability in nesting density of the Western Bluebird. This species was unique among the cavity and depression nesters as the model accounting for variability in nesting density contained only climatic variables.

Individual Species Models: The variables chosen for use in this study differed considerably in their ability to predict the densities of individual species. For example, for the Solitary Vireo the best regression model explained only 19 percent of the variability in nesting density, whereas for the Gray-headed Junco the best model explained 82 percent, and even more for some of the previously discussed secondary cavity nesters. In general the independent variables we selected had somewhat better predictive power for permanent resident species than for summer residents. They explained an average of 52 percent of the variability in nesting density for the summer residents and 65 percent for the permanent residents. This difference may be due to the biological and physical conditions experienced by these birds on the wintering grounds during the non-breeding season.

For the six permanent resident species (Gray-headed Junco, Steller's Jay, Hairy Woodpecker, Mountain Chickadee, Pygmy Nuthatch, and White-breasted Nuthatch) eight biotic and two abiotic variables occurred in the models. The eight biotic variables appeared a total of 17 times whereas the abiotic variables appeared only four times.

This is in contrast to the models selected for the four summer resident species. For this group, five biotic and six abiotic variables appeared in the models. The five biotic variables appeared a total of six times and always did so with a negative sign. The six abiotic variables appeared only six times

and one half of them were positive. Using the hypergeometric distribution the ratio of habitat variables to abiotic ones for the permanent residents was significantly different from random. ($P < 0.05$). Such was not the case for the summer residents. Thus, the two categories of birds obviously respond differently to the variables used in this study.

The major difference between the two groups of birds was the large number (8) of habitat variables and the few (2) significant abiotic variables that had a predictive power for the permanent resident birds. The most common variables included trunk volume, snag density, oak importance value, oak foliage volume, sapling volume, and total foliage volume. This list is consistent with that drawn from the guild models for habitat variables. The most common abiotic variable was precipitation in the form of snow which always appeared with a negative sign for permanent residents.

Permanent resident species appear thus to be reasonably well buffered from catastrophic climatic conditions and are species that have their densities primarily set by the habitat configuration of the pine forest. The permanent resident birds are those that are most highly adapted to life in the ponderosa pine forest and may be pine specialists. They can make physiological adjustment to withstand climatic conditions and then obtain all requisites from the forest habitat.

Summer residents, in contrast, appear in the pine forest for only three months each year. When present they are probably taking advantage of a peak in productivity that occurs during this short period. If, for some reason, this potential peak does not materialize then these species are drastically affected. This seems to be especially true in the older, uncut stands (Table 7). Here the productivity peak is later than in more open stands. Summer residents are quite possibly under tight time constraints to breed quickly and leave the area. Productivity seems closely correlated with winter weather conditions,

thus explaining the reoccurrence of these variables in many of the models.

Summer residents spend much more of each year away from the breeding habitat than they do on it. Thus, they must be adapted to feed and survive in habitat-types they encounter during migration and also on the wintering ground. Many of these habitat-types will be greatly different in physiognomic configuration from the pine forest. Hutto (MS) has recently found that U. S. warblers may winter in very different habitats from those they breed in. Summer resident species must remain as generalists relative to the permanent residents because they must be opportunistic in obtaining their requisites for survival during the non-breeding season.

Interspecific Competition: Based on the above discussion one can assume that permanent residents species interact differently with one another than they do with summer residents. But, because so few partial correlation coefficients achieved statistical significance it is difficult to assess this potential difference with these data.

The only significant negative correlation was between the permanent resident Pygmy Nuthatch and the summer resident Solitary Vireo. The Solitary Vireo reaches highest densities in forests that have been heavily managed and foliage volume severely reduced. Pygmy Nuthatch densities are highest in areas where foliage volumes are high. Thus a clear pattern emerges for the interactions of these two species. Individual regression models support the above. Solitary Vireos respond negatively to absolute density of trees (Table 12) whereas Pygmy Nuthatches respond positively to total foliage volume. The low amount overall variability in density for the Solitary Vireo may be indicative of strong competitive interactions with the Pygmy Nuthatch.

Within the pecker and gleaner guild, which contains three permanent residents and four summer residents, two couplets were significant with positive signs. One of these contained two summer residents and the other a summer resident

and a permanent resident.

Within the aerial, hawking, and hovering guild, which contains only summer residents, nine couplets were positive (3 significantly so) and six were negative. Thus, no pattern emerges within this guild about how summer residents interact with one another.

Permanent residents species in other guilds also showed no clear pattern. In the pecker-hammerer-tearer guild the only significant correlation was a positive one between two permanent residents. The Gray-headed Junco, the only permanent resident member of the ground feeding guild had two couplets with positive signs and three with negative ones.

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Table 1

Study Sites Used to Build a Simulation Model of Breeding Birds of the Ponderosa
Pine Forest

Year	Study Sites							
	PNA 1/	WS 8	WS 13	WS 14	WS 17	GF	RP	MT
1973	---	---	*	*2/	*	---	---	---
1974	---	*	*	*	*	---	---	---
1975	**	*	*	*	*	---	---	---
1976	**	**	--	**	---	---	---	---
1977	---	---	--	---	---	***	***	***
1978	---	---	--	---	---	***	***	***

1/ PNA (Pearson Natural Area); WS (Beaver Creek Watersheds); GF (Gash Flat);
RP (Rocky Park); MT (Monument Tanks)

2/ * = Szaro and Balda (1979)

Table 2

Members of the Foraging Guilds of the
Ponderosa Pine Forest

Pickers and Gleaners

House Wren
Mountain Chickadee
Pygmy Nuthatch
Solitary Vireo
Yellow-rumped Warbler
Grace's Warbler
Red-faced Warbler
Western Tanager
Hepatic Tanager

Aerial Feeders

Mountain Bluebird
Broad-tailed Hummingbird
Western Wood Pewee
Say's Phoebe
Western Flycatcher
Violet-green Swallow
Western Bluebird
Common Nighthawk

Ground Feeders

Mourning Dove
Rock Wren
Robin
Hermit Thrush
Gray-headed Junco
Rufous-sided Towhee
Chipping Sparrow

Peckers, Hammerers and Tearers

Common Flicker
Hairy Woodpecker
Acorn Woodpecker
Steller's Jay
White-breasted Nuthatch
Black-headed Grosbeck

Table 3

Results of Multiple Regression Analysis of Breeding Density Against Factors of Weather: three years

1973-1975 at WS 17 (Bird data from Szaro and Balda, 1979).

<u>Dependent Variable</u>	<u>Variability Explained (%)</u>	<u>Model</u>
Pecker-Gleaner Guild	99.0	Density = $3.352 + 2.675$ (Maximum January temperature)
Ground Foraging Guild	99.9	= $32.40 - 1.617$ (Maximum January temperature)
Pecker-Hammerer-Tearer Guild	99.6	= $28.85 - 0.2542$ (Snow)
Hawker-Hoverer-Aerial Guild	100.0	= $33.62 - 0.3365$ (Snow)
Total Bird Density	99.8	= $78.44 + 11.01$ (Winter mean daily temperature)

Table 4

Results of Multiple Regression Analysis Breeding Bird Density Against Factors of Weather: three years
1973-1975 at WS 14 (Bird data from Szaro and Balda, 1979).

<u>Dependent Variable</u>	<u>Variability Explained (%)</u>	<u>Model</u>
Pecker-Gleaner Guild	99.7	Density = $61.63 + 19.17$ (Winter mean daily temperature)
Ground Foraging Guild	99.9	= $44.26 + 11.70$ (Winter mean daily temperature)
Pecker-Hammerer-Tearer Guild	99.9	= $34.73 - 0.2251$ (Yearly precipitation)
Hawker-Hoverer-Aerial Guild	100.0	= $53.90 - 0.3946$ (Winter precipitation)
Total Bird Density	99.7	= $215.4 - 2.568$ (Snow)

Table 5

Results of Multiple Regression Analysis of Breeding Bird Density Against Factors of Weather: three years
1973-1975 at WS 13 (Bird data from Szaro and Balda, 1979).

<u>Dependent Variable</u>	<u>Variability Explained (%)</u>	<u>Model</u>
Pecker-Gleaner Guild	98.3	Density = $50.85 + 12.87(\text{Winter mean daily temperature})$
Ground Foraging Guild	100.0	= $31.90 - 0.6064(\text{Rain})$
Pecker-Hammerer-Tearer Guild	99.6	= $36.78 + 13.01(\text{Winter mean daily temperature})$
Hawker-Hoverer-Aerial Guild	100.0	= $41.00 + 11.00(\text{Yearly mean daily temperature})$
Total Bird Density	99.9	= $154.3 + 43.71(\text{Winter mean daily temperature})$

Results of Regression Analysis of Total Breeding Bird Density and Diversity Against Weather and Foliage Structure.

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>												
Total Bird Density	86.57	Density = 340.843 + 0.0018 (Total Foliage Volume) - 9.500 (Trunk Volume) - 1.925 (Oak Importance Value) - 1.198 (Precipitation as Snow) + 0.228 (Snag Denisty)												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Total Foliage Volume</td><td>43.48</td></tr><tr><td>Trunk Volume</td><td>27.19</td></tr><tr><td>Oak Importance Volume</td><td>9.25</td></tr><tr><td>Precipitation as Snow</td><td>2.44</td></tr><tr><td>Snag Density</td><td></td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Total Foliage Volume	43.48	Trunk Volume	27.19	Oak Importance Volume	9.25	Precipitation as Snow	2.44	Snag Density	
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Total Foliage Volume	43.48													
Trunk Volume	27.19													
Oak Importance Volume	9.25													
Precipitation as Snow	2.44													
Snag Density														
Total Bird Diversity	68.53	= 42.26 - 0.1075 (Precipitation as Snow) - 0.9298 (Temperature Range During Previous July through January)												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Precipitation as Snow</td><td>48.39</td></tr><tr><td>Temperature Range During Previous July through January</td><td>23.29</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Precipitation as Snow	48.39	Temperature Range During Previous July through January	23.29						
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Precipitation as Snow	48.39													
Temperature Range During Previous July through January	23.29													

Table 7

Effect of Winter Weather on the Presence of Summer Residents and Permanent Residents on Three Ponderosa Pine Plots.

	<u>Watershed Plots</u>		
<u>Permanent Residents</u>	<u>17</u>	<u>14</u>	<u>13</u>
Number of Changes (%)*	5(31)	3(21)	2(14)
Number of Species Changing	4(50)	2(29)	2(29)
<u>Summer Residents</u>			
Number of Changes	5(21)	9(28)	9(30)
Number of Species Changing	5(42)	6(38)	7(47)

*Percent of possible changes

Table 8

Results of Regression Analysis of Total Foraging Guild Density Against Weather and Foliage Structure.

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>												
Picker and Gleaner Guild	88.37	Density = 10.06 + .00020 (Total Folaige Volume) - 3.200 (Trunk Volume) + 0.284 (Snag Density) + 4.820 (Sapling Volume) - 0.639 (Precipitation as Rain)												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Total Foliage Volume</td><td>52.19</td></tr><tr><td>Trunk Volume</td><td>22.22</td></tr><tr><td>Snag Density</td><td>10.68</td></tr><tr><td>Sapling Volume</td><td>5.50</td></tr><tr><td>Precipitation as Rain</td><td>2.60</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Total Foliage Volume	52.19	Trunk Volume	22.22	Snag Density	10.68	Sapling Volume	5.50	Precipitation as Rain	2.60
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Total Foliage Volume	52.19													
Trunk Volume	22.22													
Snag Density	10.68													
Sapling Volume	5.50													
Precipitation as Rain	2.60													
Ground Feeders	59.69	=-26.587 + 0.278 (Ponderosa Importance Value) - 0.358 (Precipitation as Snow)												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Ponderosa Pine Importance Value</td><td>37.68</td></tr><tr><td>Precipitation as Snow</td><td>26.28</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Ponderosa Pine Importance Value	37.68	Precipitation as Snow	26.28						
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Ponderosa Pine Importance Value	37.68													
Precipitation as Snow	26.28													

Table 8 Continued

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>												
Peckers, Hammerers and Tearers	62.95	Density = 12.966 - 0.165 (Total Precipitation) - 1.158 (Minimum January Temperature) + 1.400 (Maximum January Temperature).												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Total Precipitation</td><td>46.90</td></tr><tr><td>Minimum January Temperature</td><td>11.14</td></tr><tr><td>Maximum January Temperature</td><td>10.40</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Total Precipitation	46.90	Minimum January Temperature	11.14	Maximum January Temperature	10.40				
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Total Precipitation	46.90													
Minimum January Temperature	11.14													
Maximum January Temperature	10.40													
Hawkers, Hoverers, and Aerial Feeders	83.96	=177.339 + 0.0020 (Ponderosa Importance Value) - 0.147 (Precipitation as Snow) -30.257 (Yearly Mean Temperature) +29.509 (Winter Mean Temperature) - 6.301 (Minimum January Temperature).												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Ponderosa Pine Importance Value</td><td>36.51</td></tr><tr><td>Precipitation as Snow</td><td>24.13</td></tr><tr><td>Yearly Mean Daily Temperature</td><td>6.54</td></tr><tr><td>Winter Mean Daily Temperature</td><td>12.90</td></tr><tr><td>Minimum January Temperature</td><td>7.90</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Ponderosa Pine Importance Value	36.51	Precipitation as Snow	24.13	Yearly Mean Daily Temperature	6.54	Winter Mean Daily Temperature	12.90	Minimum January Temperature	7.90
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Ponderosa Pine Importance Value	36.51													
Precipitation as Snow	24.13													
Yearly Mean Daily Temperature	6.54													
Winter Mean Daily Temperature	12.90													
Minimum January Temperature	7.90													

Table 9

Results of Regression Analysis of Total Nesting Guild Against Weather and Foliage Structure.

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>												
Cavity and Depression Nesters	92.79	Density = 268.788 - 2.217 (Oak Importance Value) -8.173 (Trunk Volume) -2.527 (Sapling Volume) +8.343 (Winter Mean Temperature) +0.237 (Snag Density)												
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Oak Importance Value</td><td>50.67</td></tr><tr><td>Trunk Volume</td><td>23.44</td></tr><tr><td>Sapling Volume</td><td>12.34</td></tr><tr><td>Winter Mean Daily Temperature</td><td>4.10</td></tr><tr><td>Snag Density</td><td>4.10</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Oak Importance Value	50.67	Trunk Volume	23.44	Sapling Volume	12.34	Winter Mean Daily Temperature	4.10	Snag Density	4.10
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>													
Oak Importance Value	50.67													
Trunk Volume	23.44													
Sapling Volume	12.34													
Winter Mean Daily Temperature	4.10													
Snag Density	4.10													
Foliage Nesters	69.49	= -269.911 - 0.768 (Precipitation as Snow) +1.203 (Ponderosa Importance Value) +249.481 (Proportion of Oak to Total Foliage Volume) +0.00055 (Total Foliage Volume)												

Table 9 Continued

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>
Foliage Nesters	69.49	<u>Independent Variables</u> <u>R² change (%) Unadjusted</u> Precipitation as Snow 38.92 Ponderosa Pine Importance Value 23.13 Proportion of Oak to Total Foliage Volume 8.73 Total Foliage Volume 4.82
Ground Nesters	62.21	= 29.617 + 0.058 (Ponderosa Importance Value) - 0.248 (Precipitation as Snow) - 2.644 (Yearly Mean Temperature) + 0.032 (Snag Density) <u>Independent Variables</u> <u>R² change (%) Unadjusted</u> Ponderosa Pine Importance Value 25.75 Precipitation as Snow 19.49 Yearly Mean Temperature 15.21 Snag Density 9.32

Table 10

Percent (r^2) of the Variability in Breeding Bird Density Explained by each of the Significant Habitat Variables.

Bird Species	Variables												Total
	*FV	SD	SSV	ADP	MA	MD	FV ²	SD ²	SSV ²	ADP ²	MA ²	MD ²	
Violet-green Swallow	64.5	63.1	-	-	-	-	58.5	69.0	-	-	-	-	94.4
Pygmy Nuthatch	64.2	73.9	-	-	-	-	-	-	-	-	-	-	84.7
Mountain Chickadee	28.0	60.6	50.8	-	-	-	24.2	-	-	-	-	-	87.4
Brown Creeper	-	48.6	57.7	-	-	-	-	-	72.2	-	-	-	89.3
Western Bluebird	-	-	-	16.9	16.6	16.0	-	-	-	17.5	16.6	16.6	78.0
White-breasted Nuthatch	-	-	-	-	-	-	-	-	-	-	-	-	33.8

*FV = foliage volume, SD = snag density, SSV = shrub and sapling foliage volume, ADP = absolute density of ponderosa pine, MA = mean area occupied by a tree, MD = mean distance between trees.

Table 11

Results of Regression Analysis of the Densities of Five Secondary Cavity Nesting Species Against Weather and Foliage Structure

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>														
Mountain Chickadee	84.03	Density = 2.9582 + .093034 (Snag Density) -0.0018508 (Oak Foliage Volume) -0.066046 (Precipitation as Snow) +0.72755 (Sapling Volume) +0.0011229 (Foliage Volume, 0-4 meters) -0.51718 (Trunk Volume)														
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Snag Density</td><td>45.43</td></tr><tr><td>Oak Foliage Volume</td><td>17.10</td></tr><tr><td>Precipitation as Snow</td><td>8.96</td></tr><tr><td>Sapling Volume</td><td>7.91</td></tr><tr><td>Foliage Volume from 0-4 meters</td><td>6.42</td></tr><tr><td>Trunk Volume</td><td>5.21</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Snag Density	45.43	Oak Foliage Volume	17.10	Precipitation as Snow	8.96	Sapling Volume	7.91	Foliage Volume from 0-4 meters	6.42	Trunk Volume	5.21
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>															
Snag Density	45.43															
Oak Foliage Volume	17.10															
Precipitation as Snow	8.96															
Sapling Volume	7.91															
Foliage Volume from 0-4 meters	6.42															
Trunk Volume	5.21															
Pygmy Nuthatch	82.93	= 8.78 + .000468 (Total Foliage Volume) +0.10147 (Snag Density) -0.81674 (Trunk Volume)														
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Total Foliage Volume</td><td>65.42</td></tr><tr><td>Snag Density</td><td>11.99</td></tr><tr><td>Trunk Volume</td><td>8.08</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Total Foliage Volume	65.42	Snag Density	11.99	Trunk Volume	8.08						
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>															
Total Foliage Volume	65.42															
Snag Density	11.99															
Trunk Volume	8.08															

Table 11 Continued

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>
White-breasted Nuthatch	36.20	= 18.78 - .079656 (Total Foliage Volume) - .85576 (Yearly Mean Temperature)
		<u>Independent Variables</u> <u>R² change (%) Unadjusted</u>
		Total Foliage Volume 29.06
		Yearly Mean Daily Temperature 13.52
Violet-green Swallow	94.02	= 85.6 - .80712 (Oak Importance Value) - 1.8022 (Trunk Volume) - 1.8421 (Sapling Volume) - 0.01114 (Absolute Density of Trees)
		<u>Independent Variables</u> <u>R² change (%) Unadjusted</u>
		Oak Importance Value 67.18
		Trunk Volume 16.91
		Sapling Volume 9.85
		Absolute Density of Trees 1.27

Table 11 Continued

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>
Western Bluebird	55.15	<p>-18.73 + 2.267 (Maximum January Temperature) - 2.068 (Minimum January Temperature) - 0.4265 (Precipitation as Snow) + 0.191 (Total Precipitation)</p>
		<u>Independent Variables</u> <u>R² change (%) Unadjusted</u>
		Maximum January Temperature 25.09
		Minimum January Temperature 18.76
		Precipitation as Snow 12.51
		Total Precipitation 7.77

Table 12

Results of Multiple Regression Analysis of the Densities of Five Representative Species of the Ponderosa Pine Forest Against Weather and Foliage Structure

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>										
Solitary Vireo	19.07	Density = 12.58 - .07565 (Winter Precipitation) - .010198 (Absolute Density of Trees)										
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Winter Precipitation</td><td>14.56</td></tr><tr><td>Absolute Density of Trees</td><td>12.60</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Winter Precipitation	14.56	Absolute Density of Trees	12.60				
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>											
Winter Precipitation	14.56											
Absolute Density of Trees	12.60											
Gray-headed Junco	81.59	= 51.05 - .3901 (Oak Importance Value) - 0.92577 (Trunk Volume) - 0.59398 (Sapling Volume) - 0.0858 (Precipitation as Snow)										
		<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Oak Importance Value</td><td>54.48</td></tr><tr><td>Trunk Volume</td><td>19.06</td></tr><tr><td>Sapling Volume</td><td>8.11</td></tr><tr><td>Precipitation as Snow</td><td>3.62</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Oak Importance Value	54.48	Trunk Volume	19.06	Sapling Volume	8.11	Precipitation as Snow	3.62
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>											
Oak Importance Value	54.48											
Trunk Volume	19.06											
Sapling Volume	8.11											
Precipitation as Snow	3.62											
Chipping Sparrow	43.64	= - 3.47 + 1.567 (Yearly Mean Daily Temperature) - 0.0208 (Snag Density)										

Table 12 Continued

<u>Dependent Variable</u>	<u>Variability Explained (%) (Adjusted R²)</u>	<u>Model</u>										
Chipping Sparrow	43.64	<table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Yearly Mean Daily Temperature</td><td>31.54</td></tr><tr><td>Snag Density</td><td>17.73</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Yearly Mean Daily Temperature	31.54	Snag Density	17.73				
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>											
Yearly Mean Daily Temperature	31.54											
Snag Density	17.73											
Hairy Woodpecker	29.79	<p>= 8.64 - .2438 (Trunk Volume) - .04613 (Oak Importance Value)</p> <table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Trunk Volume</td><td>23.78</td></tr><tr><td>Oak Importance Value</td><td>13.03</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Trunk Volume	23.78	Oak Importance Value	13.03				
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>											
Trunk Volume	23.78											
Oak Importance Value	13.03											
Stellar's Jay	76.54	<p>= 9.17 - .1304 (Precipitation as Snow) +0.00644 (Absolute Density of Trees) -0.011211 (Snag Density) -0.000247 (Oak Foliage Volume)</p> <table><tr><th><u>Independent Variables</u></th><th><u>R² change (%) Unadjusted</u></th></tr><tr><td>Precipitation as Snow</td><td>61.08</td></tr><tr><td>Snag Density</td><td>8.31</td></tr><tr><td>Absolute Density of Trees</td><td>7.74</td></tr><tr><td>Oak Foliage Volume</td><td>4.10</td></tr></table>	<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>	Precipitation as Snow	61.08	Snag Density	8.31	Absolute Density of Trees	7.74	Oak Foliage Volume	4.10
<u>Independent Variables</u>	<u>R² change (%) Unadjusted</u>											
Precipitation as Snow	61.08											
Snag Density	8.31											
Absolute Density of Trees	7.74											
Oak Foliage Volume	4.10											

Table 13. Partial Correlation Coefficients of Reciprocal Density Changes Between Members of the Picker-Gleaner Foraging Guild. () Significance level for each pair.

	GRACE*	WBN	WTAN	MTN	PYG	SOL	YEL
GRACE		.1498 (.362)	.4177 (.152)	.5579 (.075)	.1810 (.334)	.1480 (.363)	.0895 (.417)
WBN			-.4088 (.157)	-.3578 (.172)	.5442 (.065)	.6047 <u>(.042)</u>	.3015 (.215)
WTAN				-.1543 (.346)	.2205 (.284)	.2571 (.252)	.6543 <u>(.028)</u>
MTN					.3725 (.182)	.4707 (.120)	-.0059 (.494)
PYG						-.7930 <u>(.009)</u>	.1886 (.327)
SOL							.0818 (.424)
YEL							

*Grace's Warbler
 White-breasted Nuthatch
 Western Tanager
 Mountain Chickadee
 Pygmy Nuthatch
 Solitary Vireo
 Yellow-rumped (Audubon's) Warbler

Table 14. Partial Correlation Coefficients of Reciprocal Density Changes Between Members of the Peckers, Hammerers, and Tearers Guild. () Significance level for each pair.

	FLC*	GROS	HAIR	JAY	WBN
FLC		-.0313 (.466)	.7257 <u>(.009)</u>	-.0407 (.456)	.0499 (.446)
GROS			-.0180 (.480)	.4993 (.071)	.3426 (.166)
HAIR				.2984 (.201)	.0596 (.435)
JAY					.0585 (.436)
WBN					

*Common Flicker
 Black-headed Grosbeak
 Hairy Woodpecker
 Steller's Jay
 White-breasted Nuthatch

Table 15. Partial Correlation Coefficients of Reciprocal Density Changes Between Members of the Aerial, Hawking, and Hovering Guild. () Significance level for each pair.

	BRD*	NIGHT	VIO	WBLUE	WFLY	WPE
BRD		.8268 (.003)	-.4675 (.102)	.2937 (.222)	.5091 (.081)	.3524 (.176)
NIGHT			.4228 (.128)	-.1336 (.366)	-.4745 (.098)	-.3450 (.182)
VIO				.4969 (.087)	.9164 (.001)	-.0962 (.403)
WBLUE					.3790 (.157)	.5821 (.050)
WFLY						-.1439 (.356)
WPE						

*Broad-tailed Hummingbird
Common Nighthawk
Violet-green Swallow
Western Bluebird
Western Flycatcher
Western Wood Pewee

Table 16. Partial Correlation Coefficient of Reciprocal Density Changes Between Members of the Ground Feeding Guild. () Significance level for each pair.

	CHP*	DOVE	GRAY	HER	RCK	ROB
CHP		-.1018 (.397)	.5243 (.074)	-.0967 (.402)	.2155 (.289)	.5983 <u>(.044)</u>
DOVE			-.2071 (.296)	.2204 (.284)	-.0440 (.455)	.0771 (.422)
GRAY				.3224 (.199)	-.4644 (.104)	-.1612 (.339)
HER					.0685 (.430)	-.2446 (.263)
RCK						.4293 (.124)
ROB						

*Chipping Sparrow
Mourning Dove
Gray-headed Junco
Hermit Thrush
Rock Wren
Robin